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Mating behaviour of *Ctenomys mendocinus* (Rodentia, Ctenomyidae)

By S. Camín

Unidad de Zoología y Ecología Animal, Instituto Argentino de Investigaciones de Zonas Aridas, Consejo Nacional de Investigaciones Científicas y Tecnológicas, Mendoza, Argentina

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Abstract

This is the first description of mating behaviour in *Ctenomys mendocinus*. Observations were conducted in a transparent acrylic pipe, under dim red light. The description of the courtship and copulation stages was based on 18 trials (7 males, 9 females, 17 couples).

The mating behaviour of *Ctenomys mendocinus* was characterized by vocalizations, long courtship, long bouts of precopulatory interactions, lengthy intromissions, a brief copulation stage, aggressive copulatory postures, and mutual indifference after ejaculation. The mating and copulation patterns in *Ctenomys mendocinus* are similar to those of other solitary subterranean, phylogenetically unrelated, forms (e. g., *Spalax* and geomyids). This suggests that the copulatory behaviour of *C. mendocinus* is closely related to its social structure. On the other hand, the structure of precopulatory interactions in *C. mendocinus* is very much like that of some solitary and social bathyergids, possibly reflecting phylogenetic affinities.

Key words: *Ctenomys mendocinus*, copulatory behaviour, social biology

Introduction

The "tuco-tuco" *Ctenomys mendocinus* is a hystricomorph, fossorial, solitary rodent, and a seasonal breeder (Puig et al. 1992; Rosi et al. 1992), widely distributed throughout Argentina (Cabrera 1961; Honacki et al. 1982). In Mendoza province this species is found in different mountain environments and occurs in isolated groups of low density (Rosi et al. 1992). Our knowledge of the reproductive behaviour of the genus in general and of *Ctenomys mendocinus* in particular is limited. The only data on copulatory behaviour of the genus *Ctenomys* are those of Altuna et al. (1991), corresponding to *Ctenomys pearsoni* of Uruguay. As far as *C. mendocinus* is concerned, its mating and copulatory patterns are unknown. In her review on the patterns of behaviour of hystricomorph rodents, Kleiman (1974) regarded brief copulations as one of the typical behaviours in this sub-order. Hickman (1982) compared copulatory behaviour in *Cryptomys hottentotus* to that described for other subterranean rodents: *Spalax* (Nevo 1969) and geomyids (Andersen 1978; Schramm 1961). The differences (spontaneous nature of copulation and short intromissions in *Cryptomys hottentotus* vs. long courtship and long duration of intromissions in *Spalax* and geomyids) were explained by differences in social biology and burrow systems (social vs. solitary; copulations not restricted to particular areas vs. mating in specially constructed widened areas) (Hickman 1982). In contrast, Burda (1989) suggested that the basic characteristics of copulatory behaviour in *Cryptomys hottentotus* may relate to the common mating patterns exhibited by most hystricomorphs, and hence the differ-

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ences may also be phylogenetic. The hystricomorph condition of *Ctenomys mendocinus*, as well as its fossorial and solitary habits, led to the investigation whether its copulatory behaviour reflects its social system or its phylogenetic affinities. If this behaviour were linked with the social structure, *C. mendocinus* would differ from social subterranean hystricomorphs by exhibiting longer courtship, aggressive copulatory postures, lengthy intromissions, and aggressiveness or indifference toward the partner after mating. On the contrary, no differences would be apparent between *C. mendocinus*, and social hystricomorphs if its behaviour were mostly determined by the common, phylogenetically determined, mating pattern of hystricomorphs. Dewsbury (1972) established four attributes for a comparative study of copulation in mammals: First, the male and female may or may not become firmly locked or tied together by a strong mechanical connection during copulation. Second, pelvic thrusting may or may not occur during insertion. Third, multiple insertions with no sperm transfer may or may not be prerequisite to the occurrence of ejaculation. Fourth, either a single ejaculation or multiple ejaculations might be attained (Dewsbury 1972). As each of these four attributes has two alternatives, patterns of copulatory behaviour elaborated in this scheme can take any of 16 forms (Dewsbury 1972).

Therefore, the main goals of this study were: a) to describe the mating behaviour of *C. mendocinus*, b) to assess whether its copulatory behaviour is consistent with Hickman's (1982) hypothesis, and c) to define the Dewsburian (1972) copulatory pattern in *C. mendocinus*.

Material and methods

A total of 29 adults (16 females: 130–197 g; 13 males: 156–328 g) was live-trapped in Cacheuta (Province of Mendoza, Argentina, 1330 m a.s.l) during March for five successive years (1992–1996).

The animals were housed in a basement which received sunlight through a long narrow window above ground level. They were individually kept in plastic containers (50 cm wide × 40 cm high × 70 cm long) filled with alluvial soil to a depth of 3 cm. A 30-cm long, 9-cm diameter plastic pipe was provided for shelter. Temperatures ranged between 14 °C and 20 °C. Alfalfa, carrots, and lettuce were supplied ad libitum. No free water was provided. During June–August, males and females were periodically placed together in a transparent acrylic pipe (200×11×16 cm). Trials were conducted in dim red light between 10:00 and 14:00 h. The female was placed in the pipe 45 minutes before introducing the male. Trials started when the male was introduced into the pipe, and pairs were permitted approximately 1–1.5 h to initiate copulation. If copulation was initiated, observations were continued until attainment of the standard satiety criterion of 30 min with no intromissions (Dewsbury 1975). All trials were video-taped. Trials observed totalled 174. Only trials with occurrence of copulations were considered in the analysis of mating behaviour. Therefore, the description of courtship and copulation was based only on the 18 trials in which copulation was attained (7 males, 9 females, 17 couples). Data are expressed as mean values (±SD) and/or ranges (mini.–max. values recorded).

Results

Mating patterns recorded in *Ctenomys mendocinus* are given in table 1. Both males and females were active from the start, seeking and slowly approaching each other, growling in a low-pitched voice. Some males and one female alternated growls with whines. Some males rubbed their perineal region against the pipe walls, and sometimes urinated (Fig. 1). On finding the urine of a female, males touched it with their nose for a few seconds. Upon encounters, partners sniffed at each other's genitalia, parted, and met again to engage in precopulatory interactions: with their mouths in right angles and their incisors locked together they swayed from side to side. On occasions this swaying movement made one of the animals fall on its back thus exposing abdomen and genitalia to the part-

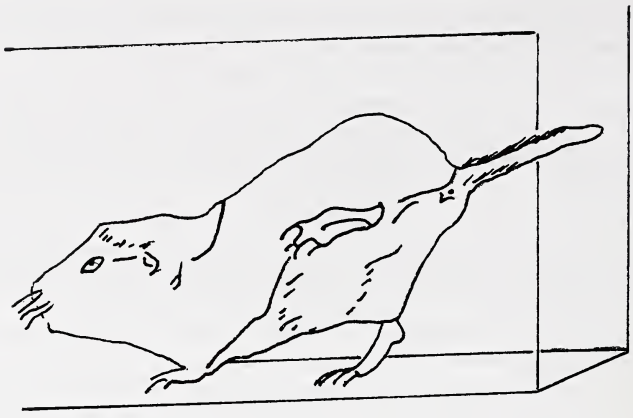

Fig. 1. Scent-marking behaviour of male of *C. mendocinus.*

Fig. 2. Mating foreplay of *C. mendocinus.*

ner (Fig. 2). The animals also stood on their hindfeet grasping each other's cheek with forefeet and teeth. This playful behaviour ended when one of the partners moved away. Some soliciting females mounted the males in much the same way as males mount females. A few females were initially inactive, reluctant to initiate courtship. They remained crouched, and exposed their incisors, ready to bite, when males came too close. Males responded to this threatening behaviour by presenting the side of the neck, half-closing the eyes and running away. In those cases where a male insisted on mounting a reluctant female, the female drove him back after a short fight. After fights like these, a few males emitted the guttural "tuc-tuc" sound typical of tuco-tucos before resuming courtship. The courtship stage was long (maximum duration: 3 900 sec, Tab. 1) and not continuous: partners played, parted, met again, and upon re-encounter courtship was resumed. First mounts occurred less than 8 min after the trial was started (Tab. 1), and were usually unsuccessful because of female resistance. In successful mounts the male mounted the female from behind, clasping her shoulders or lumbar region with his forefeet and biting her neck (Fig. 3). Occasionally the male held the female's hindfeet with his own. The female crawled away to escape, sometimes even carrying the male on her back. At first the male performed rapid shallow pelvic thrusts (PT), mostly without intromission, at a rate of 4 to 5 thrusts/sec. When the male achieved intromission, thrusts were deeper (DT) and slower (1 thrust/sec). Ejaculation, reached at the end of a number of deep thrusts, was obvious: the male grasped the female more strongly and a long lasting deeper thrust of 14 sec was discernible (SD = 10.01, range = 5–41), after which he dismounted slowly, and groomed his genitalia with forefeet and mouth.

Fig. 3. Copulatory posture of *C. mendocinus.*

Table 1. Mean duration ($\overline{X}$), standard deviation (SD), range, frequency (f) and number of observations (N) of mating and copulation patterns in *Ctenomys mendocinus.*

	$\overline{X}$ (sec)	SD (sec)	range (sec)	f	N
Mount latency	468	894	10–3 900		18
Intromission latency	616	905	14–3 900		18
Courtship	847	1056	60–3 900		18
Precopulatory interactions	44	74	2–437	4	74
Pelvic Thrusts (PT)	27	33	3–154	1	24
Deep Thrusts (DT)	53	31	5–130	1	24
Copulation	105	77	25–327	1	18
Copulation stage	256	200	40–777		18

Only two males whined during copulation, and one female uttered a high-pitched squeak as the male exercised his last thrust. Courtship was feebly resumed for a few minutes after copulation (Tab. 1), the animals walking up and down the pipe, growling and only occasionally locking their incisors until partners lost interest, and either crouched several centimeters apart or tried to escape by scratching the pipe walls until the end of the trial. A multiple-ejaculation pattern was absent in every trial. All episodes were ended by a single ejaculation. On nine of the trials ejaculation was achieved by the first mount with intromission. The remaining nine trials involved more than one mount but ejaculation was always attained on the last one. Mounting frequency was 2 (range 1–5), and the copulation stage lasted, at the most, 777 sec (Tab. 1).

Discussion

The mating behaviour of *C. mendocinus* was characterized by vocalizations, long courtship, long bouts of precopulatory interactions, a lengthy intromission, a brief copulation stage, aggressive copulatory postures, and mutual indifference after ejaculation. Tuco-tuco females did not show any typical soliciting behaviour (e. g. lordosis), yet they were active, frequently starting the precopulatory interactions and occasionally mounting the male.

As in other subterranean mammals, chemical (Nevo et al. 1976; Gorman and Stone 1989, 1990; Burda et al. 1990; Heth et al. 1992; Menzies et al. 1992) and chemosensory perception (Heth and Todrank 1995) can be very important in *Ctenomys mendocinus.*

Table 2. Mating and copulation patterns in hystricomorph and other subterranean rodents of different social structures.

Species	Courtship Length (sec)	Ejaculatory Intromission Length (sec)	Copulatory Posture	Post-mating behaviour of partners	Social structure	Sub-order	References
Geomys bursarius		15	aggressive		Solitary	Sciuromorpha	Schramm (1961)
Thomomys talpoides		30–900	aggressive	male rebuffed	Solitary	Sciuromorpha	Andersen (1978)
Spalax ehrenbergi	480–3 300		aggressive	male indifferent	Solitary	Myomorpha	Nevo (1969)
Georychus capensis				male chased	Solitary	Hystricomorpha	Bennett and Jarvis (1988 a)
Cryptomys hottentotus	30	1–5	clumsy	soliciting female	Social	Hystricomorpha	Hickman (1982)
Cryptomys damarensis		30		male not chased	Social	Hystricomorpha	Bennett and Jarvis (1988 b); Bennett (1990)
Cryptomys mechowi		brief		female pulling away from the male	Social	Hystricomorpha	Bennett and Aguilar (1995)
Heterocephalus glaber		<15	clumsy	soliciting female	Highly Social	Hystricomorpha	Jarvis (1991)
Ctenomys mendocinus	60–3 900	25–327	aggressive	mutual indifferenence	Solitary	Hystricomorpha	This study

Tuco-tuco males become informed about the reproductive status of females by contacting the urine with their noses. The posture taken by males while rubbing their anogenital region allows them to mark the walls of their burrows, resembling the behaviour of *Spalacopus* i. e. urinating on vertical surfaces using a leg lift (Kleiman 1974). Vocal communication is involved in mating behaviour of solitary species, e. g. *Spalax* (Nevo et al. 1987; Heth et al. 1987). In *Ctenomys pearsoni* only females whine, which indicates their full receptivity to courtship (Francéscoli 1995). Growls and whines in *Ctenomys mendocinus* are a signal of non-aggressiveness, and indicative of the animals' willingness to copulate. Their long bouts of precopulatory interactions help to coordinate the mating behaviour, disminishing the partners' fear and hesitation. Notwithstanding, precopulatory interactions might also play an important role in mating assessment, not just synchronisation of motivational states.

The courtship of the solitary hystricomorph rodent *Ctenomys mendocinus* was longer than that of the social hystricomorph *Cryptomys hottentotus* (Hickman 1982), whereas it was similar in length to the courtship of the solitary myomorph *Spalax ehrenbergi* (Nevo 1969). Likewise, the duration of ejaculatory intromissions of *C. mendocinus* was similar to that of the solitary sciuromorph *Thomomys talpoides* (Andersen 1978) but longer than

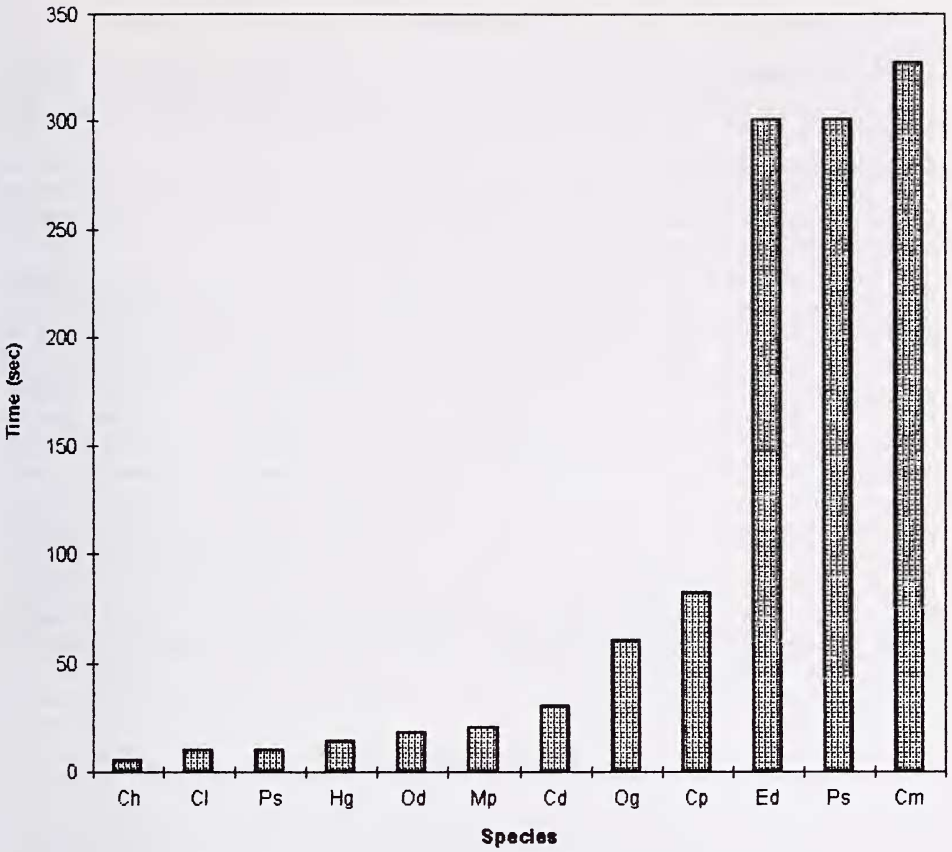

Fig. 4. Maximum duration of ejaculatory mounts in *Ctenomys mendocinus* and other hystricomorph rodents expressed in seconds. Abbreviations: Ch = *Cryptomys hottentotus* (Hickman 1982), Cl = *Chinchilla laniger* (Bignami and Beach 1968), Ps = Pediolagus salinicola (in Kleiman 1974), Hg = *Heterocephalus glaber* (Jarvis 1991), Od = *Octodon degus* (Kleiman 1974), Mp = *Myoprocta pratti* (Kleiman 1971), Cd = Cryptomys damarensis (Bennett and Jarvis 1988 b), Og = *Octodontomys gliroides* (Kleiman 1974), Cp = *Ctenomys pearsoni* (Altuna et al. 1991), Ed = *Erethizon dorsatum* (Shadle 1946), Ps = *Proechimys semi-spinosus* (Maliniak and Eisenberg 1971), Cm = *Ctenomys mendocinus* (present study).

the duration in social hystricomorphs, such as *Cryptomys hottentotus* (Hickman 1982), *Cryptomys damarensis* (Bennett and Jarvis 1988 b; Bennett 1990), *Heterocephalus glaber* (Jarvis 1991), and also the solitary sciuromorph *Geomys bursarius* (Schramm 1961) (Tab. 2). The long ejaculatory intromission of some solitary hystricomorphs like *Ctenomys mendocinus*, *Erethizon dorsatum* (Shadle 1946), and *Proechimys semispinosus* (Maliniak and Eisenberg 1971) (Fig. 4) would be exceptions to the basic pattern of hystricomorph rodents reported by Kleiman (1974), which involves brief copulations 5–10 sec long. On the other hand, mating and copulation patterns of *C. mendocinus* are consistent with Hickman's (1982) predictions according to which solitary subterranean rodents show long courtship, aggressiveness and lengthy intromissions during copulatory behaviour. This evidence suggests that the copulatory behaviour of *C. mendocinus* is more closely related to social structure (solitary life) than to phylogeny.

On the other hand, the structure of precopulatory interactions in *C. mendocinus* (e. g. locked incisors) is very much like the precopulatory interactions in *Georychus capensis* (Jarvis and Bennett 1991), the playful behaviour of *Cryptomys hottentotus* (Burda 1989), the incisor fencing between young of *Heterocephalus glaber* (Lacey et al. 1991) and sparring between young of *Cryptomys damarensis* (Bennett and Jarvis 1988 b), possibly reflecting phylogenetic affinities.

As previously stated, Dewsbury (1972) established four attributes for a comparative study of copulation in mammals based in the presence or absence of lock, intravaginal thrusting, multiple intromissions, and multiple ejaculations.

C. mendocinus failed to exhibit lock, but it did show intravaginal thrusts. Although more than one mount with intromission was required in four of 18 tests, this appears to be attributable to the resistance offered by females in such occasions. As to whether an episode may either be terminated or not by a single ejaculation, it is likely that there will be more overlap between these two alternatives than for the first three criteria (Dewsbury 1972). Although *C. mendocinus* is likely to resume copulation after the first ejaculation, in none of the 18 tests did second ejaculations occur within 30 min of the first one. The capacity to attain ejaculation on the first vaginal penetration and the absence of multiple ejaculations suggest that *C. mendocinus* conforms to pattern twelve (absence of lock, presence of intravaginal thrusting, absence of a multiple-intromission pattern, absence of a multiple-ejaculation pattern) of Dewsbury's (1972) scheme unlike *Ctenomys pearsoni* (Altuna et al. 1991), *Spalax ehrenbergi* (Nevo 1969), *Cryptomys hottentotus* (Hickman 1982), and *Thomomys talpoides* (Andersen 1978) that conform to pattern nine (absence of lock, presence of intravaginal thrusting, presence of a multiple-intromission pattern, presence of a multiple-ejaculation pattern).

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Zusammenfassung

Paarungsverhalten von Ctenomys mendocinus (Rodentia: Ctenomyidae)

Dieses ist die erste Beschreibung des Paarungsverhaltens von *Ctenomys mendocinus*. Die Beobachtungen wurden in einem durchsichtigen Rohr aus Plastik durchgeführt. Die Beschreibungen von Brunst und Kopulation basieren auf 18 Tests (7 Männchen, 9 Weibchen, 17 Begattungen). Das Paarbildungsverhalten von *Ctenomys mendocinus* war durch Beschwichtigungslaute, lange Brunst, lange Spielsequenzen, eine lange Intromissionszeit, kurze Kopulation, aggressives Kopulationsverhalten und gegenseitige Gleichgültigkeit nach der Ejakulation gekennzeichnet. Das Paarbildungs- und Kopulationsmuster von *C. mendocinus* ähnelt dem solitär und subterran lebender Gattungen, die nicht näher verwandt sind, wie *Spalax* und Geomyiden. Dieses läßt vermuten, daß das Kopulationsverhalten von *C. mendocinus* eng mit der Sozialstruktur verbunden ist. Auf der anderen Seite, ist die Spielstruktur bei *C. mendocinus*, der einiger Gattungen der Familie Bathyergidae sehr ähnlich. Dieses spiegelt sehr wahrscheinlich hystricomorphe Verwandtschaft wider.

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Author's address: Sergio Camín, Unidad de Zoología y Ecología Animal, Instituto Argentino de Investigaciones de Zonas Aridas, CC. 507, 5500, Mendoza, Argentina